oxen. The first person who kindly called our attention to those of the ox was the late Professor Pannum, of Copenhagen, who in 1874 presented us with some specimens he had found in the gall-bladder of a Danish ox.

In so far as naked eye appearances are concerned, a good specimen of the variety of pearl now spoken of is quite undistinguishable from a fine specimen of oriental oyster pearl, from its not only being globular in shape, and of a pure white colour, but from its also possessing the iridescent sheen so characteristic of oriental oyster pearls of fine quality.

In chemical composition, however, mammalian pearls bear no similarity whatever to pearls found in shell-fish, for they are composed of an organic instead of an inorganic material, namely cholesterin. In minute structure again, they bear a marked resemblance to the crystalline variety of shell-fish pearls.

The quantitative analysis of human pearls yielded in 100 parts—

| | |
|---|---|
| Water ..... | 2·05 |
| Solids ..... | 97·95 |

The solids consisted of—

| | |
|---|---|
| Cholesterin ..... | 98·63 |
| Animal matter..... | 1·37 |

From this it is seen that human pearls are in reality nothing more nor less than exceedingly pure cholesterin biliary concretions.

This note on the chemical composition of pearls is intended as a prelude to a paper we purpose shortly laying before the Society on the microscopic structure of the different varieties of pearls we had the honour of exhibiting sections of with the lime-light, as well as microscopic drawings, at the *soirée*, on the 8th June, 1887, and of which a detailed report was given in the 17th No. of the 'Cheltenham Ladies' College Magazine,' pp. 37—42, by J. F. Muspratt.

## IV. "On the Vertebral Chain of Birds." By W. K. Parker, F.R.S. Received March 8, 1888.

A few years ago I noticed a remarkable fact in the development of the Green Turtle (*Chelone viridis*), namely, that whilst *thirteen* myotomes are developed in the cervical region, the intercalary vertebral segments found afterwards are only *eight*.*

More recently, whilst working out the development of the vertebræ in various types of Birds, it struck me that we have in these high forms creatures in which the vertebral chain has been greatly

* See "Challenger" Reports, *Zoology*, vol. 5, Plate 1, fig. 3, pp. 48 and 50.

shortened during their *secular development*. It seems to me to be probable that the Amphibian stock from which birds arose—becoming Reptiles in their ascent, but spurning that intermediate stage—were long, eel-like forms, not dissimilar to *Amphiuma* and *Menobranchus* among the existing Urodeles. I will therefore state what evidence there is of evolutional abbreviation in the development of the species in existing Birds.

Working with Foster and Balfour's 'Elements of Embryology' beside me, I was struck with one part of their description, and with my own preparations showing the phenomenon. At page 157 we read as follows:—

"The notochord [in the Chick] is on the sixth day at the maximum of its development, the changes which it henceforward undergoes being of a retrograde character.

"From the seventh day onward it is at various points encroached upon by its investment. Constrictions are thus produced, which first make their appearance in the intervertebral portions of the sacral region. In the cervical region, according to Gegenbaur, the intervertebral portions are not constricted till the ninth day, though as early as the seventh day constrictions are visible in the vertebral portions of the lower cervical vertebræ. By the ninth and tenth days, however, all the intervertebral portions have become distinctly constricted, and at the same time in such vertebral portions there have also appeared two constrictions, giving rise to a central and to two terminal enlargements. In the space therefore corresponding to each vertebra and its appropriate intervertebral portion, there are in all four constrictions and their enlargements."

I had long ago noticed, figured, and described a similar moniliform condition in the cephalic portion of the notochord in the Chick,* and this observation set me speculating upon the dying out of the axial segmentation in the region of the skull.

Now this peculiar *secondary* and *temporary* segmentation of the notochord is not equal throughout the whole chain of rudimentary vertebræ; I can only find *two beads* in the sacral region, and *none* in the caudal.

Nevertheless, taking these beadings as a true historical record of development, and allowing for them in such a bird as the Common Swan (*Cygnus olor*), we get, hypothetically, a very long ancestral form. In that bird there are thirty presacral, twenty-one sacral, and thirteen caudal vertebræ that are developed as distinct vertebral segments of the axis. Then, if we treble the presacrals and double the sacrals, we add eighty-one to the actual sixty-four of the modern bird, and thus obtain *more than twelve dozen*—145—vertebræ with which to accredit the ancestral form.

* 'Phil. Trans,' 1869, Plate 81, figs. 2 and 7, and Plate 82, fig. 3, p. 771.

*On the Number of Vertebræ in Existing Birds.*

The Swan, one of the noblest of the *Precocial* birds, comes the nearest of any of the Carinatæ to the huge, almost wingless Struthious types in the large number of its vertebræ; indeed in the cervical region it has more vertebræ than any bird I have yet examined, namely, *twenty-five*, and its general sacral region is as long as in the large Ratitæ, so that this bird, although so exquisitely specialised as a flying, swimming, sailing, and walking bird, has not departed very far from the Struthious birds in respect of the length of the spine. More than this, in my recent researches into the development of this and cognate birds, I find that the Swan has been built upon the Struthious foundation—so to speak. In the parts that suspend themselves from the twenty-one sacral vertebræ, the hip-girdle moieties, it is most clearly seen that the difference in these parts between this bird and the African Ostrich (*Struthio camelus*) is altogether one of gentle transformation by a *late growth* of cartilage. Arrest the pelvis of the embryo Swan, when only two-thirds ripe, and in the ossification afterwards unite the *pubes* by ankylosis, and then the two pelves would correspond, point by point. So that this part of the skeleton passes in the most orderly manner, first through a general Reptilian, then through an Ornithoscelidan, and then through a Struthious stage, before it takes on the characteristic form of the Swan, the pelvis of which is one of the largest and most remarkable in the class, and quite typical, nevertheless, as the pelvis of a Carinate bird.

Returning to the Vertebral Chain, I may now show how, for adaptive purposes, that series of axial segments gets shorter and shorter as we ascend towards the smallest and highest of the "Altrices," the highest kind of birds, with tender young, and, as a rule, arboreal nidification.

Even within the limits of the Anatidæ, the family to which the Swan belongs, the cervical and sacral series get reduced to about three-fourths the number found in the Common Swan. Indeed, in the genus *Cygnus*, itself, I find a variation, for in *C. nigricollis* there are only twenty-four cervical vertebræ.

But among the larger Precocial birds the number varies extremely, and in passing from species to species, in the Cranes (Gruidæ), I find no two alike in this respect. Once, however, amongst the noblest and most intelligent of all the birds, the Passerines, and we come upon a uniformity that is as remarkable as the variety seen in the wading, and land, and water birds.

The Crows stand at the top of the Passerines, and being the largest kind, they have the longest vertebral chain.

In the old* Rook or Carrion Crow (*Corvus frugilegus* and *C. corone*),

* The fledgling is more generalised, and has twelve vertebræ united by the diapophyses in the sacral series.

the vertebral series is *twenty* in the presacral region, or only two-thirds as many as in the Common Swan, eleven in the sacral region, or half as many as are enclosed by *the ilia* in the Swan, whose first *caudal* corresponds with the last sacral of many birds.

Instead of sixty-four, I can only find forty-two vertebræ developed in a Crow, twenty pre-sacrals, eleven sacrals, and eleven caudals.

Now taking a familiar bird, the Common Chat (*Pratincola rubetra*), I find that it has only nineteen presacrals, eleven sacrals, and originally eleven caudals, but only *seven* distinct in the adult. Now we get in the *cervical region* in this little bird, *fourteen* vertebræ, one less than in the Crow, little more than half as many as in the Swan, and just twice as many as in the normal Mammal.

I take up the next that comes, the Yellow Wagtail (*Budytes rayi*), and it has the same number as the Chat; and, indeed, in only one species of Passerine bird, namely, *Petroica bicolor*,* from Western Australia, are there only *sixteen* free vertebræ in front of the *compound sacrum*.

As a rule, however, in the lesser birds of this Order the number is marvellously uniform, and agrees with what I have given above.

But the lesser species of Passerines amount in number to nearly one-third of the known species in the whole Class of the Carinatæ.

If it could be shown that the lesser singing birds had come up directly from the low ancestral forms, they yet suggest a rather long spine for that ancestor. It might have possessed ninety vertebræ. But I have by me most satisfactory proofs that the highest singing birds came through a series of forms that are traceable towards the Struthious birds, until, at last, I have no doubt of their merging into them.

The Passerines from the Notogæa, both east and west, have among them various genera that come short of the excellence of the general Arctogæal types. This is seen in the structure of their skulls, and in their vocal organs, and in the lower grade of their intelligence, whilst in the "Pteroptochidæ," the sternum itself—a sort of *anchor* to the classifier, which is very safe and sure in all the Passerines except in two or three genera—gives way at last, and in those birds has *five metasternal processes instead of three*.

In the smallest of all birds—the Humming-birds—the actual number of vertebræ varies very little from what is found in the lesser Passerines, but they are generally disposed of in a different manner; they may have as many as four pairs of developed ribs in the fore part of the sacrum, as in the largest kind (*Patagona gigas*); in lesser forms, as *Heliostrypha parzudakii*, *Diplogenia hesperus*, and also in the long-

* See Owen, 'Osteol. Catal. Mus. Coll. Surg.,' vol. 1, p. 299, No. 1584.

billed *Docimastes ensifer*,* I find only *three*. In the lesser Passerines, as a rule, only *one* pair of sacral ribs are developed.

*On the Articulation of the Vertebræ in Birds.*

Special modification of the vertebral chain takes place to a greater extent in birds than in any other of the Vertebrata. Even in the intensely modified vertebræ of Serpents, with their *zygosphene* and *zygantrum*, we still have merely the "procœlous" articulation of the centra.

But in birds, as soon as the *short-tailed forms* appear, we have as in Marsh's gigantic *Hesperornis*, or feeble-winged Colymbine Grebe with pleurodont teeth—the highest known form of the vertebral articulation, namely, the "cylindroidal" or "heterocœlous." This most accurate mode of locking the vertebral segments together, in which the centra viewed from below seem to be procœlous, but seen endwise or laterally are opisthocœlous, is peculiar, as far as I know, to birds, and apparently was not always, or from the beginning, present in them. This seems to be shown by the fact that the other of Marsh's toothed birds, namely, *Ichthyornis*, has for the most part "amphicœlous" vertebræ, only one or two joints at the upper part of the neck showing the cylindroidal articulation, and that imperfectly.

Now this is a most puzzling fact in Palæontology, for *Ichthyornis* is a Carinate bird, and as far as I can see, is the parent form of the Gulls (Laridæ), although it possesses *thecodont teeth* in its long jaws. Everyone knows that the Loons and Grebes (*Colymbus*, *Podilymbus*, and *Podiceps*) are "Pygopods," and rather of a low type, but the Gulls are amongst the noblest and most intelligent of the Palmipeds, and are *semi-altricial* in their breeding.

Now it is a fact that modern Grebes and Loons disagree with the other Pygopods in having all their presacral vertebræ cylindroidal, whilst the Alcidæ and the Penguins (Spheniscidæ) and Gulls have their dorsal vertebræ opisthocœlous. More than this, by careful examination of the fore end of the first sacral (*dorso-sacral*) vertebra in the lesser Gulls (*Larus canus*, *L. ridibundus*, *L. tridactylus*), I find that this is not a *ball* to fit accurately into the *cup* of the last free dorsal, but that its facet is sinuous, and does leave some space inside the joint.

Hence I infer, cautiously, but with some considerable degree of confidence, that the modern Gulls have not quite perfected even the lower or "opisthocœlous" form of articulation of the vertebral centra for *all* their dorsals.

I call the opisthocœlous mode of articulation *lower*, because it certainly comes short in type of the cylindroidal, and is I believe the

* In that bird, which is much smaller than *Patagona*, the whole skull is $5\frac{1}{3}$ inches long (137 mm.), and the rest of the axis $2\frac{1}{4}$ inches (56 mm).

more common kind of articulation in Archaic Reptiles, whilst the "procœlous" mode is almost universal in the existing Reptiles.

But, in fact, Birds are very *eclectic* in the manner in which their vertebral centra are articulated, and any kind of articulation that happens to be the best for the particular region in which it is found is selected, so to speak.

I will show, 1st, in what families the dorsal vertebræ are opisthocœlous; 2ndly, the modification in Birds of that type of articulation; and then how many sorts of articulation they exhibit in this or that Family.

In his valuable memoir on the Penguins,* the late Professor Morrison Watson greatly understates the number of Families that have this peculiarity, namely, the Penguins and the Auks. Now amongst the Steganopods or Pelicanine types they are found in the Cormorants and Darters (*Plotus*).

Amongst the Old World Pygopods this structure occurs in all the Alcidæ—*Alca*, *Uria*, *Ciceronia*, &c., and in all the Charadriomorphæ or Shore birds (Limicolæ), and in the Gulls (Laridæ, Lestridæ, &c.), but not in the Petrel tribe—Procellaridæ.

But amongst the most highly specialised arboreal "Altrices" I have long been familiar with this peculiarity in the great Parrot Family—Psittacidæ—in which, strangely enough, it is combined with a very unlooked for character, namely, with terminal epiphyses—a structure which begins to show itself in the Ornithorhynchus, in the caudal region.

This is very remarkable in these high, hot-blooded birds, for in the whole class epiphyses are very rare, *only one* being constant; this is found in the *cnemial crest* of the tibia.

But the Parrots are not the only high kinds of birds in which the dorsal vertebræ are opisthocœlous; I have within the last two years found it in that remarkable type, the Oil Bird (*Steatornis caripensis*), an *archaic*, *frugivorous Goat-sucker*—a bird which has no near allies, a crepuscular Cave-dweller, found only in Cumana and a neighbouring island, and manifestly a waif from a nearly lost group.

*On the Modification of the Opisthocœlian Articulation in Birds.*

The *cup* and *ball* in these opisthocœlous dorsals of birds is very different from what is found in the procœlous vertebræ of the Ophidia; in them it is fairly circular or hemispherical, whilst in birds it is generally scarcely more than three-fifths of an ellipse, and the upper margin is emarginate, having a concave outline answering to the general concavity of the floor of the spinal canal.

That which shows such intense specialisation in the procœlous vertebræ of the Serpents is the remarkable manner in which an

* "Challenger" Reports, *Zoology*, vol. 7, p. 16.

additional upper pair of confluent pre-zygapophyses form what Owen calls a "zygosphene;" this fits into a double cavity—the "zygantrum."

Now the articulation of the opisthocœlous dorsals of the birds thus mentioned is a complication of the articulation of centrum with centrum, and not any special modification, in their case, of the neural arch from which the zygapophyses spring.

In Reptiles, as far as I can see, whether existing, or otherwise, there is nothing like what I am about to describe; if any Palæontologist will show me a similar structure I shall be most glad to know of it. Such a fact would tell us how carefully these highly metamorphosed types, the Birds, have kept along Reptilian lines; if not, if no such structure as this, any more than the cylindroidal articulation, is ever seen in Reptiles, then we have another instance of the manner in which the Birds have proceeded beyond the excellencies of their progenitors.

The greatest perfection of this complex opisthocœlian articulation of the dorsal vertebræ is best seen in some remarkable Charadrian birds; three of which are Neotropical, whilst one is found in Kerguelen's Island; I refer to *Chionis*, *Attagis*, and *Thinocorus*.

In *Attagis gayi*, a Neotropical bird of the Plover family, stouter than a Lapwing, but about the same size, a nearly extinct type, and very archaic, I find the best instance of this Ornithic modification of the opisthocœlian articulation of the dorsal vertebræ. On the hind face of the centrum the *cup* in its fresh state is heart-shaped; it is half a long ellipse, with its upper edge gently emarginate. There is a strong annular "meniscus," 1·5 mm. deep below, and 0·6 mm. wide for the rest of its extent. It is a very solid fibro-cartilage, except for a small extent above, where it is finished by a ligamentous part. When this meniscus, which partly divides the joint cavity into two spaces, is removed, the hollow cartilaginous tract is seen to be in three parts; below, a semicircular hollow, marked in its middle by the notochordal "suspensory ligament," and above, on each side, a flat ear-shaped additional facet. These two facets look equally downwards and backwards, and they lie obliquely on a similar pair of facets over the ball on the fore-end of the centrum of the next vertebra which looks upwards and forwards. These well-fitting oblique facets, fore and aft, are, indeed, additional zygapophyses, arising not from the neural arch, but from the centrum; and they check the movement of the cup-and-ball joint. For a bird needs not only a very long and absolutely ankylosed sacrum, it must also have a very strong dorsal series; not unfrequently all but the last of this series are also ankylosed together; this only takes place in birds which have their dorsals cylindroidal.

*On the Presence of Procœlous Vertebræ in Birds, and of the Imperfect and Irregular Joints between the Centra.*

The modern procœlous Reptilian form of vertebral articulation is not altogether wanting in Birds. The atlas, although devoid of its proper centrum, forms a more or less perfect joint of this kind in all birds; it is crescentic in many of the Precoces, and circular in most of the Altrices; and in the latter it is not notched above for the "odontoid or suspensory ligament," but perforated.

But in many of the higher or Altricial birds the last two movable joints in the caudal series become procœlous, and also acquire a joint-cavity. The rest of that series have a sub-concave joint, with an intervertebral fibro-cartilage filling in the slight interspace; these joints, however, retain the suspensory ligament like all the rest, and towards the end of this series the centrum is perforated by this remnant of the notochord, as in lower types.

The joint formed by the hind part of the *atlas* and fore-part of the *axis* is irregular; it cannot be classified with any of the other modes of articulation, but this arises from the fact that it is formed between the cortical or inferior part only of those two vertebræ. The two first vertebræ are greatly modified in all the "Amniota," an anticipation of which is found in the Urodelous Amphibia.*

There are two main varieties, in Carinate birds, of the articulation of the atlas with the occipital condyle, and of the atlas with the axis.

These correspond on the whole with the Natural Division of birds into "Altrices" and "Precoces"; the Piping Crow of Australia (*Gymnorhina tibicen*) may be taken as an example of the first, and the Australian Bustard (*Eupodotis australis*) of the second kind.

In *Gymnorhina* the atlantal (procœlous) cup is a perfect hemisphere, but near its upper rim the suspensory ligament passes through a small hole to reach the basi-occipital. This cup fits well under the hemispherical occipital condyle; it is in position intermediate between that condyle and the true atlantal centrum. The hind face of this imperfect vertebral body is scooped so as to form a crescentic groove, with the concavity upwards; the convex fore-end of the axis fits into this groove, and the atlas grows under the joint as a bilobate and carinate process; the joint is a *crescentic condyle* with its concavity looking upwards.

* In many of these there is an imperfect vertebra between that which is articulated with the two occipital condyles; it is evidently an *atlas* with an imperfect neural arch, and the median and lateral elements of which become fused to form the odontoid process. The perfect vertebra next following is evidently the *axis*, but has the atlantal function of carrying the skull. See Wiedersheim, 'On *Salamandrina perspicillata*,' Genoa, 1875, Plates 2—4, and my papers, "On the Skulls of the Urodeles," 'Linn. Soc. Trans.,' Ser. 2, Zool., vol. 2, Plates 14—21, and 'Zool. Soc. Trans.,' vol. 9, Plate 40.

In *Eupodotis* the procœlous facet of the atlas is a crescent with horns approximating, and between these the odontoid process, or true atlantal centrum, appears; it is embraced by these "horns," and, as in the other type, is tied to the basi-occipital by the suspensory ligament. In this bird, contrary to the rule, the atlas does not grow under the axis, and the joint between them is almost procœlous; and in this and still more in some other Precoces, the occipital articulation is transversely enlarged, *i.e.*, shows signs of being double, as in Amphibia, the *notochordal dimple* answering to the wide interspace between the condyles in these forms.

I shall explain these things more perfectly when I come to the "intercentra."

The *imperfect joints* are those of the sacrum and the coccygeal bones. The long general sacrum of a bird does not correspond to the special sacrum of a Reptile or a Mammal, and in the dorsal region of this long series the articulations are, at first, like those of the free dorsals in front of them; *i.e.*, they are cylindroidal or opisthocœlous, as the case may be. But as we approach the true sacral region, between the acetabula, the faces of the centra are roughly flat, and the centra themselves are transverse subcrescentic blocks, with all the intercentral structures aborted.

The same thing takes place in the *ploughshare* or coccygeal bone, which finishes the chain by a series of from *four to six*, more and more imperfect, segments, from which, for a time, in the embryo the notochord projects, uncovered, behind.

There are other ankylosed parts of the vertebral chain besides the sacrum and the coccygeal bone; in these the parts are normal at first, becoming afterwards fused together. It is very common for the last cervical (whose free rib does not unite by a short piece with the sternum) to be fused with the dorsals—all but the last, which remains free, as in Falcons, Pigeons, Fowls, &c. The same thing takes place in many of the Crane family, but generally with fewer bones. In the Hornbills (Buceridæ) the atlas and axis become ankylosed. In some other Altrices we have there found that which is normally the last free dorsal fused with the first of the dorso-sacral series; and in others the first dorsal sacral, covered by the iliac bones, remains free; this is, however, a very irregular modification, and is sometimes due to old age in one case, and to a somewhat immature condition in the other.

In the present paper I cannot go into details as to the various modifications of the neural arches, with their zygapophyses and spines, nor describe the various outgrowths below that arise from the centra. But there are *distinct parts* of the vertebra that must be mentioned; these are the "intercentra" and ribs.

*On the Intercentra of Birds.*

I have not spoken of the neural arches as actually distinct from the centra; they are, as bony tracts, for a time, but the great *heat* and *haste* of the development of an embryo bird causes many essentially distinct parts to be converted into hyaline cartilage continuously; such distinct morphological regions, however, are very apt to assert their independence for a few weeks during the growth of the young bird, and although separate osseous centres in a continuous tract of hyaline cartilage are apt to be very inconstant as to the share they take in the work, yet, on the whole, in default of the primary segmentation of the cartilage, they are very valuable landmarks.

In a survey of this subject from below upwards, it is well known that the neural arches come before the centra; that establishes their independence and importance.

It is very difficult to put this matter into a small compass, and to show throughout the whole of the Vertebrata what parts of a vertebra are important autogenous "elements" and what are mere *apophyses* or outgrowths. The *old pre-embryological nomenclature* fails us here, entirely.

Nothing *newer* and nothing *better* has been said upon this subject than by Baur, whose wide acquaintance with the extinct forms that lie between Birds above, and Fishes below, makes him, on the whole, an excellent guide.

In some "General Notes" [extracted from the 'American Naturalist,' October, 1887, pp. 942—945] Dr. Baur (p. 945) gives his "results" as follows:—

"1. That the ribs are *intervertebral.*

"2. The ribs are originally one-headed and connected with well-developed intercentra.

"3. All forms and connexions of the other ribs can be derived from that condition.

"4. The lower arches of the caudal vertebræ are either formed by true ribs, the oldest fishes (Ganoidei, Dipnoi), or by processes of the intercentra (Teleostei, Stapedifera).

"5. The connexion between the Dipnoi and the Stapedifera is still missing.

"6. Some remarks on the nomenclature of the elements of the vertebral column:—

"Owen's names, 'neurapophysis' and 'pleurapophysis,' are not correct; the neural and pleural arches are no processes of the vertebræ, but are distinct parts.

"The two elements composing the neural arch ought to be called the '*neuroids*,' the two elements composing the pleural arch the '*pleuroids*.'

"The spines connected with the neuroids ought to be called, as before, *neural spines*; those connected with the pleuroids, *pleural spines*.

"The real centrum of the vertebra ought to be called *centrum;* the lateral elements composing it *hemicentra* (Albrecht), not pleurocentra.

"The name intercentrum ought to be preserved.

"The part of the intercentrum, centrum, or neuroid to which the capitulum is articulated, may retain the name *parapophysis*; the part of the centrum or neuroid to which the tuberculum is articulated may retain the name *diapophysis*."

If we consider the structure of a bird as compared with a Reptile or a long-tailed Mammal, it would seem to have no necessity for the development of "chevron-bones" or *intercentra*; yet these elements are constantly present at the two extremities of the vertebral chain, although in the hind-part they are often not more developed than those seen in the lumbar region of the Mole (*Talpa europœa*).

If all birds have come up to us through forms similar to the *Archœopteryx*, then there must have been a slow, secular degradation of these inferior arches: that view, however, places the Toothed Birds of the Cretaceous Period as far from those Saururous types as the Birds of the present time.

That the aquatic, gill-bearing forms from which, originally, the Reptile and the Bird both arose were long-tailed, I have not the least doubt. One thing, however, I never can see, and that is that there was any absolute necessity that there should be *just one pair* of those old quasi-larval Dipnoans (or Amphibians) that had, at that immeasurably remote epoch, "the promise and potency" of all those Reptiles and Birds that *we know* have arisen, and of all those myriads of others of which we know nothing.

As the times became ripe for the harvest of scaly and feathered forms, they did appear, but had they all one father and one mother?

Another question to be asked is, Were there ever any *per saltum* rises in the scale; did all those nobler and still nobler forms acquire their varying degrees of excellency, from a low Reptile to a high Singing-bird, by the slow accretion of growth, and almost imperceptible change of structure, and increase of faculty?

It would greatly relieve my mind if it could be shown that the most probable hypothesis is that the swarm of old Perennibranchiates in a thousand places, and at varying times, changed for the better; became sometimes rapidly, at other times more slowly, transformed as the occasions arose; when the dilemma was *transform or die*. That is the dilemma, now, to all our native Amphibia year by year, and that which takes place now in forms that rapidly rise to

a great height above their former selves, may have taken place in the past on a grander scale, and with centuries for days.

However it came about, the *Saururous* (*long-tailed*) forms have become *Nothurous*, have a mere *bastard tail* or stump. Yet this morphological feat is performed in the transformation of any Tadpole in "a month of days," hence the real difficulty does not lie with Nature, but with us.

But in studying the abortive chevron-bones of birds we shall find that these high and marvellously transformed types are not short-tailed, if we consider *number* merely; it is the peculiar contraction and *packing*—consolidation—these segments have undergone that make them to differ so greatly from Reptiles and Saururous birds.*

In the Common Swan (*Cygnus olor*), behind the four true sacrals there are ten "urosacrals" fused with the long *post-ilia*; then come seven simple, and one compound, bone, composed in the *cygnet* of five bony segments and an unossified rudiment behind, six altogether. We thus get, even allowing for four sacrals, twenty-three vertebræ, more or less developed behind the outgoing sacral nerves, whilst the *Archæopteryx* appears to have had only twenty-one caudal vertebræ (See 'Zool. Soc. Proc.,' 1863, p. 517).

Now of these post-sacral vertebræ of the Swan nearly the hinder half have rudimentary intercentra. These are very small, those in the middle of the series being the largest. In the cygnet about a month after hatching, the first is beneath the third movable joint, and the last under the last cartilaginous interspace but one, in the series of imperfect segments that form the "ploughshare bone;" thus there are *eight* in all.

But there are intercentra at the other end of the chain; these I have studied in the Cygnet, in the ripe embryo of the Mooruk (*Casuarius bennettii*) and in various other birds, especially Carinatæ; whilst my son (T. J. Parker) has worked them out in the embryo of *Apteryx*. In these embyo, and young birds, there are always found the following osseous centres in the atlas and axis, namely, a pair for the neural arch of each vertebra, and one for the so-called "body" of the atlas, one for the odontoid process of the axis, and two for the body of the axis, not right and left, but *one before the other*.

The osseous centre in the cartilaginous odontoid process is strung upon the notochord, like the rest of the centra; it is the specialised

* This subject has long been on my mind; lately Dr. Baur unearthed an almost forgotten paper of mine on the tail of modern birds. See his "W. K. Parker's Bemerkungen über Archæopteryx, 1864, und seine Zusammenstellung der hauptsächlichsten Litteratur über diesen Vogel," 'Zool. Anzeiger,' No. 216, 1886. My earliest paper on this special point was read at the Zoological Society on December 8, 1863. See 'Zool. Soc. Proc.,' 1863, pp. 511—518. It was "On the Position of the Crested Screamer (*Palamedea* [*Chauna*] *chavaria*)."

and segmented centrum of the atlas, whilst the much larger bony centre to which it is attached, and which also is strung upon the notochord, is the centrum of the axis; they coalesce together, according to the rule, a *new* rule and part of the general transformation of an Amniotic type. But the so-called body of the atlas is in position between as well as below the occipital articulation, and is *cortical*. The lesser and foremost bone in the axis is also intermediate between as well as below the true centrum of the atlas and of the axis. I quite agree with Baur that these two bones are *intercentra*, although I am not ready with the "strong reasons" he can bring from every corner of Palæontology.

In considering both *intercentra* and *ribs*, there are two birds that have helped me most; these are the Swan and the Cormorant (*Phalacrocorax carbo*).

Whether faster or more slowly, the transformation of these two types from a Reptilian into an Avian form is certainly well worthy of our closest attention. The Ostrich tribe, a sort of half-way creatures, only help a little in this research; yet in tracing the stages of a Swan or of any other of the Anatidæ, there would appear to be nothing strange in the sudden arrest of one at the Struthious stage; we seem for a time to have before us a new kind of short-legged and web-footed bird of the Ostrich kind; *it does move*, however, it develops into a Carinate bird with a Desmognathous palate. I lay stress upon this, because, as I shall soon show, the Anatidæ hold with the Ratitæ in the matter of a perfect series of cervical ribs, as in the Crocodile, but more aborted, and soon fused with the vertebræ. Birds are very uniform, in all essentials, in their atlas and axis; but their caudal vertebræ differ just as much as the structures they support differ, *e.g.*, the "Rectrices," or tail quills, that form their double, fan-shaped, *third wing*.

The Cormorant puts its tail to a much greater variety of uses than the Swan; the component vertebræ of the former are stronger and have much larger intercentra to serve as levers to the *depressors* of the tail.

There are two movable caudals between the post-ilia in the Cormorant, and the second of these has a seed-like intercentrum that lies below and between the second caudal articulation. The next is much larger, and the rest are as long and twice as broad as the neural spines of the same vertebræ, and are ankylosed to the hinder bone; they lie well under the one in front, and form the lower third of the procœlous joint. The last or compound bone has *four* of these intercentra fused together and to the imperfect vertebræ to which they belong; thus this bone has a dilated and dentate base, the fore-part of which passes under three-fourths of the last simple vertebra, and is bilobate, whilst those in front are clavate. In some birds these intercentra have

two crura, and these may meet below and form a *hæmal canal*; in the Cormorant they are solid, and are manifestly developed for *steering* purposes—as in the Kestrel or Windhover (*Falco tinnunculus*). The habits of that voracious, rapid, and powerful bird (the Cormorant) explain the teleology of these strong and solid intercentra of the tail.

Coming now to the *ribs*, my two chosen types, the Swan and the Cormorant, will be the best instances to show how thin the partition is between a hot-blooded bird, and a cold-blooded *generalised* Reptile, like the Crocodile. In my earlier papers on the Osteology of Birds, I wrote in a general and somewhat confused manner about *reptilian characters* in Birds; but Professor Huxley's inestimable paper "On the Classification of Birds" ('Zool. Soc. Proc.,' 1867, pp. 415—472), so thoroughly ventilated the relations of the two great classes, Reptiles and Birds, showing indeed that in a very true sense the two were one, a huge double class—base below and noble above—that if I am confused now, it is not the fault of my "guide."

It is perfectly true that the Ratitæ, on the whole, are the lowest, most generalised, and most reptilian of birds; but they have a high degree of ornithic specialisation in some parts, much beyond what is seen in some other birds that, on the whole, belong to a much higher level.

Now the Ratitæ are related to a large number of families of birds, that like themselves have cylindroidal vertebræ up to the sacrum; and there is an almost natural and complete series of these forms, Tinamous, Hemipods, Fowls, &c., &c. But as I showed many years ago, the Duck-tribe and the Fowl-tribe have a skull which is fundamentally alike in both groups, and is unlike that of any other kind of bird's skull, and yet is easily derivable from the Struthious type, by this and that gentle metamorphic alteration.

But if the Cormorant and his relatives were each derived from Ratitæ, *they* must have been quite unlike those now existing; a Swan, strange as the assertion may sound, is modified from an essentially Struthious embryo. I have traced it step by step.

But the Cormorant, and the Darter (*Plotus*), its nearest relative, seem more like a survival of transformed Plesiosaurs, and their Vertebral Chain is so intensely Reptilian that, among living forms, the Crocodile is the best guide to the morphologist in its interpretation.

### *On the Ribs of Birds.*

I will first describe the ribs of the Swan, and then those of the Cormorant.

In *Cygnus olor*, as in all the normal "Chenomorphæ," the vertebral artery, right and left, runs inside a series of bridges, which, eked out by strong membrane, form a canal all along the neck. The piers of these small bridges are formed by the upper and lower transverse

processes (*diapophyses* and *parapophyses*); the arches by arrested ribs—"pleuroids." As a rule, in the Carinatæ, these are not developed on the *axis* and *atlas;* but in the Anatidæ, as in the Ratitæ, generally, they are found in them also. The arch on the atlas is a strong but narrow bar; in the Cygnet of a month old there is in it a styloid bony rib, placed subvertically. The rest are larger, are horizontally placed, and have a free styloid end, which in many cases almost reaches to the end of the centrum of the next vertebra. These *riblets* have but little primary independence as cartilages; but they ossify separately; they are clavate, and this clubbed fore-end has thus no distinction of "capitulum" and "tuberculum," although the lower edge answers to the one, and the upper to the other.

In the twenty-second vertebra the styloid part is lost, and only a broad vertical bridge is developed by the "pleuroid;" in the twenty-third only a narrow bridge, like that on the *atlas*, but stouter. On the twenty-fourth and twenty-fifth the ribs are segmented off, have double heads, and remain free, although they do not form a perfect arch by reaching the sternum; indeed the last but one is very short. In these two vertebræ the facet for the capitulum is on the centrum, opposite the lower part of the facet of the centrum; that for the tuberculum is on the diapophysis. Thence along the five free dorsals and the two first dorso-sacrals, the joint for the tuberculum (the parapophysis) gets gradually higher, so that in the two last it lies over where the suture was between the centrum and neurapophysis. The developed ribs of the third and fourth sacral (dorso-sacral), have lost their capitulum, and articulate only by their tuberculum on the diapophysis.

The last three vertebræ of the seven that buttress the *pre-ilia*, have only a generalised mass, right and left; and on the next four, the true sacrals, these are either gone, or reduced to mere prickles. The twelfth and thirteenth have strong pleural bars, not segmented off in the cartilaginous condition, but they are ossified as distinct bars; these coalesce with the centrum and diapophysis. Behind these, in the Cygnet, there are no "pleuroids," but in a recently hatched Duckling (*Anas boschas, domesticus*), I find *five* pairs of these little *rib-bars* to the fore-half of the Urosacral series.

Thus there are *thirty-four* pairs of ribs, rudimentary or developed, without a break, in the Common Swan, and then an attempt at forming a new series behind the sacral nerves. Also, let it be noticed, that the first two pairs of pleuroids, or rib-rudiments, *arise from intercentra*, whilst the last two of the twenty-nine have lost their capitulum, or primary head, and are articulated by their tuberculum or secondary head to the diapophysis, an outgrowth of the neural arch (neuroid).

Thus we have in a single vertebral chain an epitome of the history

of the evolution of ribs. Towards the end of that chain, the vertebræ and ribs form the upper part of the most highly specialised thoracic cage in existence, it is the last consummation of the whole evolutional series, the furthest from the beginning made by the *Ammocœte*, when it has just been metamorphosed into a Lamprey.

In the Cormorant, one of the lower forms of the Pelecanine Family ("Steganopods," "Dysporomorphæ"), the vertebral chain is much more archaic than in either the Swan, or even the Ostrich and its kindred.

Here, indeed, we miss the atlantal rib, but rudiments are present on the *axis*, and these are attached to an ankylosed intercentrum.

On the whole, the greater number of the styloid cervical ribs are like those of the Swan, except that the upper edge of the free style is not connected with the neural arch by an ossified aponeurosis. There are only three presacral vertebræ that have developed ribs attached to sternal pieces, and thus forming perfect cinctures, finished below by the common inverted keystone or sternum. The ribs on the last two cervicals, the nineteenth and twentieth, have perfect heads, and have uncinate pieces attached and ankylosed to them, but their sternals are suppressed. In front of them there are three vertebræ, with non-segmented riblets, that have no retral style; these are mere *necks* of a developed rib, and run almost horizontally from the centrum to the large diapophysis; they are, in fact, similar to, but much stronger than, the atlantal rib of the Swan. The parapophysis in these three vertebræ stretches straight out from the centrum, which is also alate behind it, and these bars enclose a large foramen, 8 mm. wide and 4 mm. high. The nineteenth cervical, with its developed vertebral rib, forms for the capitulum of that rib a deep cup with two distinct facets, so that the head of the rib articulates in a manner similar to what is seen in Mammals. In them, however, the two facets are one in front of the other, and on distinct vertebræ; here they are one above the other, and near the fore-end of the same vertebra, one is on the centrum, and the other is on the neural arch. The facet on the centrum is higher than the junction of capitulum and centrum, in the non-segmented rib next in front. In the last cervical, the lower facet is still higher, but is on the centrum; both these pairs of ribs have a long neck and the normal articulation of the tuberculum with the under face of the end of the large diapophysis, an outgrowth of the neural arch.

In the three dorsals the parapophysial cup for the capitulum is entirely on the neural arch, and, from before, backwards, it keeps rising to a higher point in that arch. Thus in a few vertebræ we have the capitulum rising from a point *where the intercentrum would be* if it were developed, to a point quite clear of, and some height above, the centrum itself. The first general sacral vertebra is similar to the last

free dorsal; its vertebral rib has a perfect sternal piece, and thus there are four complete cinctures to the thorax. The last developed rib is feebler, and its sternal piece does not quite reach the sternum. There is a dia-parapophysial facet for its feeble upper part; it is a cup nearly as large as the diapophysial facet in front of it, and the cartilage lining the cup is extended downwards on a narrow convexity of the transversely carinate outgrowth, and thus this rib, with a small head, and a neck less than half the normal size, articulates by one continuous facet belonging to both tuberculum and capitulum, and entirely on the neural arch.

The third vertebra in the general sacral series has a pair of ribs; these have lost their capitulum entirely; they are mere rods, 6 mm. long and 0·75 mm. thick, and are ankylosed by their inner twisted end to the diapophyses.

After these come three pairs of strong *pre-iliac buttresses*—generalised masses, from which all trace of rudimentary ribs has gone—in the old bird. Then come two vertebræ with the bodies nearly devoid of lower outgrowths; these are the true sacrals. These are followed by the urosacrals, the first of which has strong rib-bars that buttress the *post-ilia*, and that are ossified as distinct riblets, but are not segmented off as distinct tracts of cartilage in the embryo. But in old birds the buttresses of the second true sacral are not quite absorbed, but remain as prickles, for the clearing away of unnecessary parts goes on even after the bird is adult. This is only one among many instances that could be adduced in which the transformation of the skeleton is seen to be continued throughout life. In that transformation, from beginning to end, each individual bird repeats the story of its birth in the past ages, and each individual bird seems to be striving towards some goal, albeit in its present state, when adult, its structure is to the morphologist an absolutely perfect thing.

In birds, as a rule, the true sacrals abort, or even suppress, the pleuroid rudiments in the true sacrals; four of these block-like vertebræ form the sacrum proper of the Swan; two only in the Cormorant.*

* Professor Huxley (*op. cit.*, p. 416), in this *third* character of Birds as distinguished from Reptiles, says that, "Although all birds possess a remarkably large sacrum, the vertebræ, through the intervertebral foramina of which the roots of the sacral plexus (and, consequently, of the great sciatic nerve) pass, are not provided with expanded ribs abutting against the ilium externally, and against the bodies of these vertebra by their inner ends." Those true sacrals are called 'lumbo-sacral' by Professor Mivart ('Zool. Soc. Trans.,' vol. 10, p. 345, Plate 61, fig. 1), whilst the first two "uro-sacrals" are called "sacral." This is certainly an erroneous nomenclature.

Professor Mivart speaks of his examination of the skeleton of *P. bicristatus* and *P. brasiliensis*, as well as of *P. carbo*. His figure of the pelvis is probably one of these, and not of *P carbo*; it differs from the two old specimens of the common

I shall finish this paper with one more instance. In most birds the true sacrals have only the upper transverse processes, or diapophyses; the lower bars, or arrested "pleuroids," are entirely gone in the adult, but small prickles remain, often more on one side than on the other. Thus the spaces for the large sacral nerves and their ganglia, and for the lobes of the kidneys, are not quite cleared. In the Tiger-Bittern (*Tigrisoma leucolophum*), a Neotropical member of the "Ardeidæ," there is no vertebra in the sacrum, until we come to the last three uro-sacrals, that has not its inferior or "pleuroid" bars.

The sacrum of this bird is composed of fifteen vertebræ, the first has developed ribs, with imperfect sternal pieces, the next two have small ankylosed ribs, separated for some distance from the diapophyses. Then come three with stout generalised pre-iliac buttresses. The next *six* have inferior rib-bars, those of the last four are strong, those of the first two weak. On the left side the second of these rods is membranous for a short extent; on the right side it is imperfect in its outer part, it is a mere prickle growing from the centrum. Except on the atlas this bird has ribs or rudiments of ribs up to the twelfth sacral. I suspect that if the ancestral form from which the Tiger-bittern arose could be put face to face with its stilted descendant, the two would differ as much as the vermiform larva of *Tipula oleracea* differs from its winged and stilted imago.

## V. "Second Preliminary Note on the Development of *Apteryx*." By T. Jeffery Parker, B.Sc., C.M.Z.S., Professor of Biology in the University of Otago. Communicated by W. K. Parker, F.R.S. Received March 8, 1888.

The materials for the present investigation consist of embryos of the three common species of *Apteryx*, viz., *A. australis*, *A. oweni*, and *A. mantelli*. Most of them, including all the earlier stages, were collected for me by Mr. R. Henry, of Lake Te Anau; a nearly ripe embryo of *A. mantelli* was obtained from Mr. A. Reischek: and I am indebted to Mme. Müller for a half-ripe specimen of *A. oweni*, and to Sir Walter Buller for two, somewhat older, of *A. mantelli*.

I desire to record my sincere thanks to the Council of the Royal Society for the grant which has enabled me to defray the expenses of the investigation.

My observations are far from complete, and deal only with comparatively late stages. The eggs of *Apteryx* are at all times difficult to obtain, as evidenced by their high market value, and Mr. Henry is

bird dissected by me in having the pre-ilia buttressed by *seven* pairs of massive processes instead of *six*, by having only *one* true sacral, and by showing strong costal bars on both the first and second "uro-sacral."